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A Phylogenetic Study of the Thoracic Sclerites of the Psychodoid Diptera, with Remarks on the Interrelationships of the Nematocera.

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(Plates III and IV.)

Through the kindness of Dr. J. W. Campbell and Mr. T. R. Harris, I have been able to make a study of the anatomy of such rare and primitive New Zealand Diptera as Nemopalpus. Tanyderus, etc., and Dr. C. P. Alexander has very generously permitted me to make a detailed study of the amber Dipteran Macrochile, which is in some respects the most primitive Dipteran of which we have any knowledge and presents many features common to several groups of Diptera. Mr. R. Shannon and Mr. H. S. Barber have very kindly given me a number of specimens of *Phlebotomus*, and through the kindness of Mr. F. W. Edwards, I have been able to study several other types of Psychodidae. For the specimens of Nannochorista studied, I am indebted to Dr. Campbell and Mr. Harris. Since most of the insects here figured are extremely rare and valuable, I am more than grateful to the above-mentioned gentlemen for permitting me to make this study.

The principal point brought out in this study, is the close relationship between the Ptychopteridae, Tanyderidae and Psychodidae, indicated by the thoracic sclerites. Mr. Edwards has very kindly consented to allow me to quote his statement, made in litteris, that the Tanyderidae and Psychodidae should be grouped in a single superfamily, the Psychodoidea. Just after learning of Dr. Edwards' view, I had an opportunity of making a detailed anatomical study of Macrochile contained in a collection of amber Diptera received by Dr. Alexander; and the study of Macrochile, which offers the key to the whole

situation, clearly indicates that the Ptychopteridae, Tanyderidae and Psychodidae should be grouped in a single superfamily or similar division of the Nematocerous Diptera, since Macrochile is in a sense a synthetic type combining characters occurring in the Ptychopteridae, Tanyderidae and Psychodidae. In fact, I consider that Macrochile is the nearest living representative of the common ancestor of these families, although Macrochile is itself an "out and out" Tanyderid, as Dr. Alexander points out from its venational characters—and as is indicated by its head and thoracic structures as well.

Before taking up the discussion of those features in which *Macrochile* is annectant between the rest of the Tanyderidae and the Ptychopteridae and Psychodidae, I would call attention to some of the thoracic characters which all of these insects have in common, and which indicate that they should be grouped in a single superfamily, the Psychodoidea.

In all of the Psychodoidea, the meral region of the middle coxa becomes detached from the coxa and fuses with the lower portion of the mesothoracic epimeron to form the area labelled *mpl* in all figures. The only other lower Diptera in which this occurs are the Eriopterine Tipuloids, and this fact may have some phylogenetic significance. There is a fusion of the meral region with the lower portion of the epimeron in the mesothorax of the Blepharoceridae, also, but the meron does not become detached from the coxa as in the Psychodoidea and Eriopterine Tipuloids, so that the end result in the Blepharoceridae is different, and hence has no particular phylogenetic significance.

A second feature common to all Psychodoids is the fact that the scutal suture labelled *s* in all figures is incomplete, while in the Tipuloids, and of course in the Eriopterine Tipuloids as well, the scutal suture forms the well-known "V-shaped" suture familiar to all systematists.

In practically all Psychodoids, the suture labelled *a* in all figures, is incomplete, and in all of these insects, the sclerite labelled *saf* is more or less clearly demarked.

Macrochile exhibits all of the above-mentioned features common to all Psychodoids, and in addition, it offers certain characters indicating that it is anatomically intermediate between the different Psychodoid families, and hence has departed less than any of the other forms here studied, from the condition characteristic of the common ancestor of these Psychodoid families.

Thus, in the length of the coxae, *Macrochile* (Fig. 1) is intermediate between the Tanyderid types with short coxae shown in Figs. 2 and 4, on the one hand, and the Psychodid types with extremely long coxae shown in Figs. 8 and 10, on the other; and it is approached by the Ptychopterid shown in Fig. 6. This fact taken alone, has no particular significance, since short and long types of coxae occur in some members of all three Psychodoid families, but taken in connection with the other features here mentioned, this fact does have some significance.

In the relative sizes of the prothorax, and the pronotum in particular, Macrochile (Fig. 1) is intermediate between the Tanyderid types shown in Figs. 2, 3 and 4, with their greatly elongated pronota and the Psychodid types shown in Figs. 8 and 10, with their greatly reduced pronota; and again, the condition exhibited by Macrochile is approached by that of the Ptychopterid shown in Fig. 6. In fact, the general character of the thorax of Macrochile, which is not as depressed as that of the rest of the Tanyderids, nor as elongated as that of the lower Psychodids, furnishes a more suitable "starting-point" from which these other types (and that of the Ptychopterid shown in Fig. 6, as well) could be derived, than does any other of the forms here shown; and I think that Macrochile represents more nearly than any other, the type ancestral to the Psychodoidea in general, although, of course, this does not mean that Macrochile is the actual ancestor of the Psychodoidea.

Since some Mecoptera (which are very like the ancestors of the Diptera) have a rather broad pronotum, as in the Mecopteran *Nannochorista*, shown in Fig. 5, this might be taken to indicate that the broader type of pronotum exhibited

by the Tanyderids shown in Figs. 2, 3 and 4, represents a more primitive condition than that of *Macrochile*. On the other hand, some Mecoptera also have quite narrow pronota (as in *Bittacus* and other members of the order) so that the narrow pronotum of *Macrochile* is not of necessity a specialization, and its pronotum is assuredly more like those of the rest of the Psychodoidea than is the case with pronota of the Tanyderids other than *Macrochile*.

Although the enlarged pronotum of such Tanyderids as the ones shown in Fig. 2, may not represent a specialization, the greatly elongated neck plate lc of this insect certainly seems to be a case of specialization in the direction of extreme length, when we compare this region in Tanyderus (Fig. 2) with the same region in a Mecopteran such as Nannachorista (Fig. 5), and it would seem that the elongated lateral cervical lc of the Tanyderids shown in Figs. 4 and 3 shows more specialization than does the more normal type of lateral cervical lc in the insect shown in Fig. 1. If the lateral cervical plates of these Tanyderids are more specialized than that of Macrochile, it is also possible that their pronota are likewise more specialized than that of Macrochile; and the huge pronotum of Peringueyomyina (Fig. 3) seems to indicate that there is an orthogenetic tendency in the group to develop an unusually long pronotum, so that the large pronota of these Tanyderids may possibly denote a degree of specialization rather than a retention of a condition more primitive than that exhibited by Macrochile.

Whether or not *Macrochile's* pronotum is more primitive than the pronota of the other Tanyderids, it is none the less true that *Macrochile's* pronotum is more like that of the rest of the Psychodoidea; and the rest of the Psychodoidea exhibit a marked tendency toward the reduction of the pronotum which is carried to the extreme in such Psychodoids as the one shown in Fig. 7, or in those shown in Figs. 11, 10 etc. *Macrochile* would thus offer a better "starting point" than any other Tanyderid, in attempting to trace the modification of the pronota of the Psychodoidea in general.

In regard to the metanotum, this region is extremely large

in Nemopalpus, Bruchomyia and Psychoda (i. c., the region labelled mtn in Figs. 8, 10 and 11), although in such a Psychodid as Phlebotomus (Fig. 9, mtn) it becomes markedly narrow in the median region. The metanotum mtn of Macrochile (Fig. 1) is somewhat intermediate in type between that of the Tanyderids and Psychodids, so that even in this particular also, Macrochile occupies an intermediate anatomical position in keeping with its general annectant character.

It is rather disappointing to find that Phlebotomus' metanotum is narrowed in the median region, since the combination of peculiarly broad metanotum and extremely narrowed pronotum would otherwise serve to differentiate the Psychodidae from the other Psychodoid families. The very narrow pronotum and medianly narrowed metanotum of Bittacomorpha (Fig. 7) however, would indicate that Bittacomorpha might have inherited some of the tendencies which affect the mode of development of *Phlebotomus* (Fig. 9) also, and the Psychodidae and Ptychopteridae thus exhibit in some of their members peculiar tendencies which may have been inherited from a common ancestry. The type of pronota, however, is not precisely similar in the Psychodidae and in the Ptychopteridae with reduced pronotum (Fig. 7), so that there is no difficulty in distinguishing the two groups thoracically, and the suture b, present in the Psychodids, is lacking in the Ptychopterids.

All of the Ptychopteridae which I have examined have a peculiar "prehaltere" labelled *prh* in Figs. 6 and 7. This "prehaltere" may possibly serve as an organ for detecting currents of air in flight, or for directing flight, or some similar function, although its real significance is not known. It seems to be peculiar to the Ptychopteridae, since I have seen no mention of its occurrence in other groups of Diptera, although in the Syrphidae an organ having a somewhat similar appearance occurs under the fore wing in the region of the subalar plate, but of course it is not in any sense homologous with the organ in question in the Ptychopteridae.

The location of the metathoracic spiracle extremely close to

the base of the cut-off halter in the Ptychopterids here figured is a character they share with all Psychodoids, while the very tiny mesothoracic spiracle (located just back of the pronotum) is peculiar to all the Psychodidae and the tendency toward the reduction of the mesothoracic spiracle is not shared by the rest of the Psychodoidea. It may be remarked in passing, that the mesothoracic spiracle of the Mecopteran Nannochorista (Fig. 5) is very tiny also, but the mesothoracic spiracle is proportionately much larger in the Mecopteran Bittacus.

The thoracic features indicating a close relationship between the Ptychopteridae, Tanyderidae and Psychodidae, then, are the location of the metathoracic spiracle very close to the halter, the fusion of the detached mesothoracic meron with the lower portion of the epimeron, the demarcation of the sclerite saf, and the incomplete character of the suture a, and of the suture s (of all figures). The nature of the thoracic structure would thus indicate that the Ptychopteridae, Tanyderidae and Psychodidae were descended from a common ancestry (from which Macrochile has departed but little) and should be grouped in a single superfamily, the Psychodoidea.

I formerly thought that the subfamily Bruchomyinae, placed in the Tanyderidae by Dr. Alexander, represents a distinct family, the "Bruchomyidae," but the thoracic sclerites of Bruchomyia and Nemopalpus (Figs. 10 and 8) are so similar to those of such Psychodidae as Phlebotomus (Fig. 9) that it is necessary to place the Bruchomyines in the family Psychodidae. The male genitalia, venation, etc., of Bruchomyia, however, are of a quite different type from those of Phlebotomus and Psychoda, and I would prefer to retain the subfamily Bruchomyinae instead of sinking it in the Phlebotominae as Mr. Edwards seems inclined to do.

(To be continued.)

Abbreviations.

a.....Anepisternal suture
acm....Pteropleurite or anepimerum
acs....Anepisternum